PATTERNS, CAUSES AND CONSEQUENCES OF TOOTH WEAR IN CERVIDS

VEBJØRN VEIBERG

2007

DISSERTATION FOR THE DEGREE OF PHILOSOPHIAE DOCTOR

DEPARTMENT OF BIOLOGY
FACULTY OF MATHEMATICS AND
NATURAL SCIENCES
UNIVERSITY OF OSLO
OSLO, NORWAY

DEPARTMENT OF BIOLOGY
UNIVERSITY CENTRE IN SVALBARD
LONGYEARBYEN, NORWAY

© Vebjørn Veiberg, 2007

Series of dissertations submitted to the
Faculty of Mathematics and Natural Sciences, University of Oslo.
No. 643

ISSN 1501-7710

All rights reserved. No part of this publication may be
reproduced or transmitted, in any form or by any means, without permission.

Cover: Inger Sandved Anfinsen.
Printed in Norway: AiT e-dit AS, Oslo, 2007.

Produced in co-operation with Unipub AS.
The thesis is produced by Unipub AS merely in connection with the
thesis defence. Kindly direct all inquiries regarding the thesis to the copyright
holder or the unit which grants the doctorate.

Unipub AS is owned by
The University Foundation for Student Life (SiO)

CONTENTS

PREFACE

Looking back at the time spent on this thesis is like looking back at a journey with endlessly small steps. The time has been filled with speculations, mind-wrestling, doubt and delight, and without the fruitful and stimulating collaboration with people, of whom I owe the greatest respect and thank, I would have been nowhere near my dissertation.

Of the many that deserve to be thanked, I want to start with my three supervisors: Rolf Langvatn – my UNIS supervisor and door opener. You believed that I could cope with the challenges related to a PhD, and created both the opportunity for a position and the basis for the majority of my work. You're the main person to blame for this, you know, and I will always be deep in debt for your generous goodwill and support. Nils Christian Stenseth – your working capacity and engagement as chair of CEES is nothing but impressive. I thank you for allowing me to join your group through these years, and creating the stimulating learning environment that this scientific melting pot truly is. Atle Mysterud – my friend and ever-present supervisor. Your professional clear-sightedness, moral standards and your ability to structure and pinpoint a message is admirable. Your always constructive comments, inputs and support have been invaluable.

Through nearly four years, working hours, various field trips and data gathering bouts, as well as quite a bit of leisure has been shared with Leif Egil Loe. I thank you for your hospitality, friendship and generosity. Justin Irvine, Steve Albon, Audun Stien and Erik Ropstad. Together with Rolf you have represented the core group of the Svalbard reindeer project, and faithfully generated a unique series of data that I have been allowed to benefit from. The access to roe deer and moose data were arranged by Jean-Michel Gaillard and Erling Solberg respectively. I thank you all for your goodwill and fruitful collaboration. I also need to thank the people at UNIS for your service-minded attitude, and for bearing with my long absence.

At last, Lise. My coach, wife, mistress and mother of my children, I owe you the most.

Blindern, August 2007

Vebjørn Veiberg

ABSTRACT

Foraging ecology and environmental conditions have represented important driving forces in the evolution of both dental morphology as well as the digestive system. Teeth are essential for digestive processes in ruminants, and their persistent function and durability are regarded to be of major importance to animal performance and life-history strategies. Despite their high degree of wear resistance, teeth wear as a result of extensive use over time and the abrasive properties of plant foods. This potentially reduces their functionality and may thus reduce forage utilization, energy gain and in turn affect the animal's life-history. This has to a little extent been investigated in the wild.

In this thesis I aim to study some causes and consequences of tooth wear among northern cervids. I also intend to evaluate the importance of current ecological and prior evolutionary factors as predictors for spatial patterns in tooth wear and investment.

My approach in Paper I was to quantify changes in occlusal topography, both related to age and individual body mass, and to assess its consequences for mastication efficiency. Data from the world's northernmost ungulate, the Svalbard reindeer *Rangifer tarandus platyrhynchus* Vrolik, was used to investigate these questions. Inhabiting the Arctic deserts of Svalbard, this subspecies experience extreme environmental conditions, potentially representing a stronger selection pressure on teeth than the conditions experienced by herbivores living at lower latitudes. The results showed that occlusal topography decreased steadily with age, indicating a parallel reduction in mastication efficiency. As wear increased, the proportion of small particles in the reticulo-rumen decreased, indicative of reduced digestion efficiency. Heavy animals up to approximately five years of age had more worn teeth than lighter animals of the same age. This suggests a trade-off between early growth and tooth wear. In Paper II I do a closer investigation of consequences from age-related tooth wear on reticulo-rumen retention and dimension. In addition, I also wanted to evaluate whether tooth wear could be linked to a potential reduction in energy gain. Again using the Svalbard reindeer as study species, I found that the mass of reticulo-rumen content and tissue increased with age. The increase of reticulo-rumen tissue suggests that physiological alterations occur in response to decreased mastication efficiency. Increased mass of reticulo-rumen content was likely a

combination of the tissue enlargement and the altered particle properties due to reduced mastication efficiency. The summed effect of both changes is a permanent increase in digestive capacity. Amount of back fat decreased with advancing age. This suggests that alterations in digestive processes were not sufficient to compensate for reduced mastication efficiency.

The two fenced French roe deer *Capreolus capreolus* L. populations in Chizé and Trois Fontaines experience contrasting habitat quality and differ in several life-history traits. I used tooth measurements from animals of known age to test whether habitat quality or life span was the more important factor to tooth wear rate and durability. There was no between-population difference in tooth wear rate, and thus no effect of habitat quality on tooth wear. But, animals from the area with longer lifespan expectancy possessed higher initial molars, as would be expected if teeth investment was mainly decided by life-history. This linkage between lifespan and teeth endurance is in correspondence with evolutionary predictions.

In Paper IV, I compared inter- and intraspecific rates of both incisor and molar wear in a large browser (moose *Alces alces* L., six populations) and a mixed-feeder (red deer *Cervus elaphus* L., four populations) to assess the importance of evolutionary history vs. the variation in current environmental conditions to patterns of tooth wear. The data covered both a substantial variation in environmental conditions and the main distribution area of both species in Norway. Analyses revealed that the mixed-feeder wore both incisors and molars faster than the browser, but there was no close link between incisor and molar wear rates at the population level. Although within-species tooth wear rates differed between populations, the species-specific molar wear patterns were consistent. Effect of population density was only detectable for red deer males. The results support the view that evolutionary history is responsible for the main patterns of interspecific molar wear patterns. Still, variation in environmental conditions caused variation in wear patterns within species, but this variation was much more pronounced in the mixed-feeding red deer than in the browsing moose.

In this thesis, I have demonstrated that reduced occlusal topography have consequences for digestive processes in ruminants, and argue that these changes may be likely causes of senescence. I also show how different causes (environmental conditions,

body growth patterns, feeding-types) may generate variation in tooth wear patterns within and between species. I recommend future investigations to further reveal the functional relevance of age-related tooth wear for digestive mechanisms in ruminants, and possibly to link variation in tooth wear among individuals explicitly to individual life-time fitness.

LIST OF INDIVIDUAL PAPERS

Paper I. **Veiberg, V.**, Mysterud, A., Bjørkvoll, E., Langvatn, R., Loe., L.E., Irvine, J.R., Bonenfant, C., Couweleers, F. & Stenseth, N.C. 2007. Evidence for a trade-off in early growth and tooth wear in Svalbard reindeer. Journal of Animal Ecology **76** (6): (In press)

Paper II. **Veiberg, V.**, Mysterud, A., Irvine, R.J., Sørmo, W. & Langvatn, R. Increased reticulo-rumen filling with advancing age in Svalbard reindeer: a consequence of increased retention due to worn teeth? (Submitted Journal of Zoology)

Paper III. **Veiberg, V.**, Mysterud, A. Gaillard, J.-M., Delorme, D., Van Laere, G. & Klein, F. 2007. Bigger teeth for longer life? Longevity and molar height in two roe deer populations. Biology Letters **3** (3): 268-270.

Paper IV. **Veiberg, V.**, Loe, L.E., Mysterud, A., Solberg, E.J., Langvatn, R. & Stenseth, N.C. 2007. The ecology and evolution of tooth wear in red deer and moose. Oikos (In press)

INTRODUCTION

The environment serves as the basis and the designer for all features of life (Stearns, 1992). Physiological, morphological and behavioural traits and adaptations are the results of multiple cost-benefit trade-offs, and evolve within the framework of conditions given by the surroundings. Strategies and adaptations related to energy gain and consumption are main determinants for animal life time performance. The evolution of dentition has been acknowledged as one of the major events in the evolution of vertebrates (Lucas, 2004). Well functioning teeth are essential for food capturing, ingestion and processing in all terrestrial mammals. Their durability, high degree of specialization and close link to life-history, have made teeth valuable tools in the study of evolutionary processes in foraging ecology of extinct as well as extant species. Permanent dentition – or rather the possession of a deciduous followed by a permanent set of teeth – have the great advantage of continuous functionality, which is not being periodically disrupted by loss and addition of individual teeth. Provided with permanent dentition, precise occlusion between opposing rows of interlocking molars could develop in mammals (Janis & Fortelius, 1988). The cost of such a trait is that permanent teeth gradually wear down and are not replaced. Their functional durability does therefore need to be adapted to last for the entire expected lifespan of an individual.

Plant food contains considerable less energy per unit, requires more extensive grinding to facilitate digestion, and induce more wear on the dentition (especially the molar occlusal surfaces) than animal food (Janis & Fortelius, 1988). The key to understand why plant food needs to be extensively masticated is the contents of cellulose and hemicellulose. These structural carbohydrates represent the main constituents of the plant cell walls, enclosing the easy digestible cell contents primarily composed of sugars, proteins, and storage carbohydrates. Ungulates are lacking the digestive enzymes cellulase and hemicellulase and rely on symbiotic microorganisms for degradation of the (hemi)cellulose components. Since the microorganisms are inefficient in reducing forage particle size (Spalinger &

Robbins, 1992), mechanical degradation through mastication is vital to increase surface to volume ratio of forage particles, and thereby facilitate microbial decomposition and digestion efficiency.

Among herbivores in particular, morphological adaptations that increase chewing efficiency and dental functional durability are expected to enhance individual performance, and are thus expected to have been under strong selective pressure. The evolution of high-crowned (hypsodont) cheek teeth in ungulates has been found to coincide with periods of drying climate (Fortelius *et al*., 2002; Jernvall & Fortelius, 2002). Many of the factors favouring hypsodonty tend to increase in effect with increasing aridity and opening of landscape (increased forage fibre content, increased abrasiveness from intracellular silica or extraneous dust, and decreased nutritive value) (Fortelius, 1985; Janis & Fortelius, 1988; Janis, 1988; Fortelius *et al*., 2002). Dietary preferences and ecological characteristics of habitats are main causes for substantial variation in dental dimensions and morphology found among various species (Janis, 1988). The same causal factors have also been the driving forces behind the adaptations found within the rest of the digestive system.

The evolution of teeth and their functional morphology have been thoroughly explored (e.g., Teaford, Smith & Ferguson, 2000; Lucas, 2004). Simultaneously, comparative studies of digestive morphology and the mechanisms related to digestive processes have provided detailed information on food utilization in mammalian herbivores (Demment & Van Soest, 1985; Gordon & Illius, 1994; Van Soest, 1994; Clauss & Hummel, 2005). The knowledge about the functional consequences of tooth wear in wild ruminants, and its interplay with digestion and forage utilization is scarce; although it has been repeatedly predicted (Tyler, 1987; Skogland, 1988; Kojola *et al*., 1998). Current variation in environmental conditions have generated intraspecific differences in tooth wear rates both between (Loison *et al*., 2001; Garrott *et al*., 2002) and within areas (Nussey *et al*., 2007). In addition, life-history strategies may also be responsible for differences in wear pattern between males and females, like suggested in red deer (*Cervus elaphus* L.; Carranza *et al*., 2004). Despite the common consensus

about the vital importance of dentition for efficient mastication in ruminants, limited information exists about how teeth wear with age and the functional relevance of these changes (cf. following section on tooth wear).

The overall aim of this thesis was to gain knowledge about patterns, causes and consequences of tooth wear in an assemblage of northern cervids. I do this by combining measures of tooth wear of culled individuals with data indicative of digestive processes and life-history. Specifically, I aimed to evaluate the importance of current ecological and prior evolutionary factors as predictors for spatial patterns in tooth wear and investment.

My approach in Paper I was to quantify changes in occlusal topography, both related to age and individual body mass, and assess its consequences for mastication efficiency. Paper II was a closer investigation of consequences from age-related tooth wear on reticulo-rumen retention and dimension. In that paper I also aimed at evaluating whether tooth wear could be linked to potential reductions in energy gain. Paper III and IV focus on spatial variation in inter- and intraspecific patterns of tooth wear, evaluating the importance of life-history characteristics, ecological conditions and evolutionary history.

In the following sections I will first provide some background information on herbivore tooth design, wear and functionality. Then I will turn to the ruminant digestive system – with main attention on topics of particular interest to this study – before providing an introduction to the concept of feeding types. The study systems, from where the data originate, and the methods used to extract tooth measures, will be briefly presented in a material and methods section. Subsequently, the main results from each paper will be summarized and briefly discussed, before ending with some concluding remarks. I refer to the individual papers for details.

TOOTH DESIGN, WEAR AND FUNCTIONALITY IN HERBIVORES

Tooth design

Teeth contain the most durable of all biological tissues, and has rather illustrative been described as rocks attached in the mouth (Lucas, 2004). Their main components are enamel, dentin and cementum listed after

decreasing mineral content and hardness (see, e.g., Lucas (2004) for a detailed description). Cementum, mainly covering the root of the tooth, protects the root and serves as an anchorage for the periodontal ligaments attaching the tooth to the surrounding alveolar bone for stability. The purpose for enamel and dentin is to function as the area of mastication (and therefore the area exposed to wear). Combined, their complex construction and differing properties represent a wear resistant unit. The three-dimensional occlusal tooth surface of herbivore teeth is specially designed to cope with the challenges related to efficient mastication of food items of which the animal is adapted to. Based upon cusp patterns, molars are normally categorised into three morphological groups (Fig. 1). i) *Bunodont* – rounded or pointed cusps covered with enamel (unless heavily worn). ii) *Selenodont* – complex pattern in terms of enamel-dentin infoldings and infundibuli creating crescent-shaped pools of dentin surrounded by enamel. iii) *Lophodont* – a complex pattern of elongated enamel ridges surrounding pools of dentin or cementum. These sections, lophs, may be oriented perpendicular to the tooth row or more complex.

Ungulate molars are often merely referred to as hypsodont (high-crowned). Since the degree of hypsodonty exhibits substantial interspecific differences, such a collective term easily becomes insufficient – at least within a comparative context. To distinguish between molars differing in crown height, three classes of hypsodonty are commonly used: brachyodont, mesodont and hypsodont (Fortelius *et al*., 2002). The classification is based on the ratio of height to length of the upper or lower second molar (M_2); with ratios less than 0.8 characterizing brachyodont teeth, ratios between 0.8 and 1.2 characterizing mesodont teeth, and ratios larger than 1.2 characterizing hypsodont teeth.

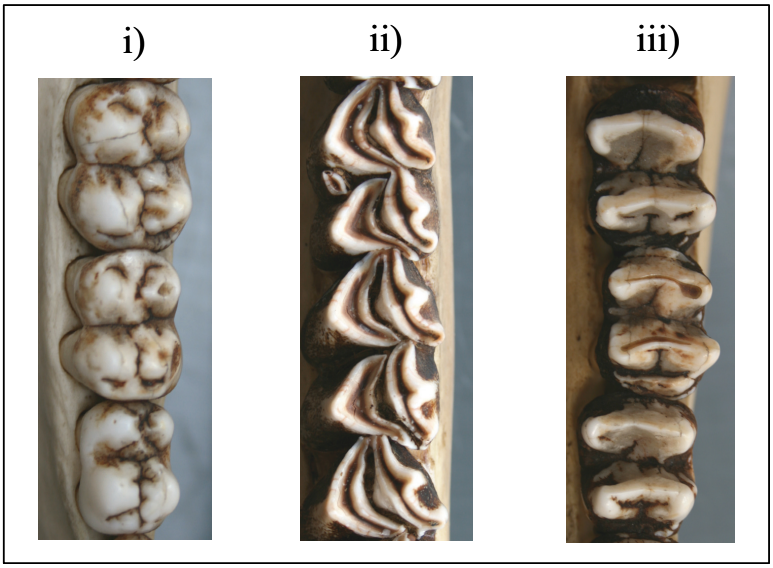

Figure 1. Three examples of occlusal morphology in mammalian cheek teeth. i) Bunodont – found in omnivorous mammals (sample picture of peccary *Tayassuidae* indet.). ii) Selenodont – found in cervids and bovids (sample picture of moose). iii) Lophodont – found in elephants, tapir and many rodents (sample picture of tapir *Tapiridae* indet.).

Functionality

The selenodont molars of ungulates are essentially non-functional in their newly erupted form, and a moderate degree of wear is required to transform the shape into its functional configuration (Luke & Lucas, 1983). Once this has been achieved, the tooth is constructed so that its shape and function is largely maintained through much of its life (Rensberger, 1988). Still, a point in time is eventually reached where the tooth ceases to grow, and the functional form rapidly degrades (Evans, 2005). The phenomenon of tooth wear is therefore likely to be important and may impose severe limitations on animal physiology and behaviour – particularly in the later life stages. However, few studies on wild cervids have investigated this explicitly.

Tooth wear

Apart from the rate of food intake, the rate of wear and the maintenance of function is dependent on the teeth morphology, the way in which they occlude and the nature of the diet (Rensberger, 1973; Perez-Barberia &

Gordon, 1998a). Dental wear may be divided into two kinds: attrition, the wear caused by the contact between opposing teeth; and abrasion, wear caused by food ground between teeth. Their collective contribution represents the overall tooth degradation. While tooth wear lack scale and is a rather general designation, mesowear denotes the wear that can be evaluated macroscopically through quantification of cusp relief and cusp shape (Fortelius & Solounias, 2000; Franz-Odendaal & Kaiser, 2003). The additional microwear consider scratches and pits observable only with a microscope (30-500 or more magnification) (Walker, Hoeck & Perez, 1978; Teaford, 1988; Merceron, Viriot & Blondel, 2004). The resolution used and the patterns studied in mesowear and microwear analyses, have been found suitable for providing information regarding dietary preferences in extinct as well as extant species.

All measures of tooth wear have their limitations with respect to their qualities as indicators in life-history related approaches. Still, tooth wear has frequently been suggested as a proximate cause of age related reduction in performance (senescence[1]) (Skogland, 1988; Ericsson & Wallin, 2001; Mysterud *et al*., 2001b; Logan & Sanson, 2002; Loe *et al*., 2003; King *et al*., 2005). The general absence of detailed quantitative measures directly linked to molar functionality has, on the other hand, prevented a closer evaluation of its actual relevance to digestive processes. This lack of quantification has typically lead to one of two alternative conclusions: i) tooth wear causes an age-related reduction in mastication efficiency (normally the case in studies concerning life-history strategies), or ii) the effect of tooth wear is regarded as insignificant (normally the case in studies concerning digestive processes). Although tooth wear is a continuous process, Perez-Barberia and Gordon (1998b) found that molar wear in red deer had a positive effect – in terms of increased mastication efficiency – until prime age, before additional wear caused gradually reduced chewing efficiency. This result adds an additional alternative relationship to the two, already, contrasting assumptions. The variety in

[1] The progressive loss of function accompanied by decreased survival and reproductive rate with increasing age.

suggested age-related relationships and factors potentially influencing food communition (Perez-Barberia & Gordon, 1998a) underlines the need for better insight in the processes and consequences related to dental wear, and to challenge the assumptions of interspecific generality in its overall patterns. The aim of Paper I is to provide a quantitative link between measurable and age-related tooth properties, and investigate its proximate consequence on mastication efficiency. Further, the consequences from differing life-history strategies (growth investment and longevity) on tooth wear, is explored in Paper I and III respectively.

HERBIVORE DIGESTIVE SYSTEMS – CONSTRAINTS AND ADVANTAGES

The greatest challenge for mammalian herbivores is how to extract a sufficient amount of energy, given the low concentrations of energy in plant food (relative to that of animal food). Two main digestive strategies have evolved in response to this ultimate challenge; hindgut fermentation and rumination (Langer, 1988). Each of the strategies has both advantages and constraints. Hindgut fermenters are adapted to consume large volumes and tolerate low rates of nutritional extraction per unit plant mass, a strategy that is favourable in periods of high abundance of low quality forage (Demment & Van Soest, 1985). Ruminants, on the other hand, are adapted to increase forage utilization through selective retention of rumen particles, delayed passage, and regurgitation and further mastication of large forage particles. This strategy is advantageous in periods of low forage availability. Focusing on the ruminants, morphological characteristics of the digestive tract have been linked to dietary preferences and used to classify species along the grazer-browser continuum (Hofmann, 1989; see also below).

The most striking feature of the digestive tract of ruminants is the division of their stomach into four easily distinguishable chambers: the rumen, the reticulum, the omasum and the abomasum (Langer, 1988, Fig. 2). The abomasum, being the only stomach compartment that contains gastric glands producing hydrochloric acid and digestive juice, is the equivalent of the simpler and more stereotypic mammalian stomach. The three remaining chambers

(collectively termed forestomach) consist of non-secretory tissue. Because of the wide opening between the rumen and the reticulum, these two compartments form one functional chamber, commonly referred to as the reticulo-rumen. The reticulo-rumen is by far the largest unit of the digestive tract and is the main site for microbial fermentation and selective retention of forage particles.

The reticulo-omasal orifice is the bottleneck for flow of digesta from the reticulo-rumen to the omasum, and was for a long time considered to be a limiting factor for reticulo-ruminal particle escape (Clauss, Lechner-Doll & Streich, 2002). The fully opened reticulo-omasal orifice diameter is, on the other hand, recognised to far exceed the threshold size for particle passage, emphasizing the importance of other retention mechanisms. The passage of any particle is therefore the combined result of possessing the right properties (specific gravity and size) and of being positioned in sufficient proximity of the orifice as it opens.

The main factors involved in selective retention are contractions of reticulo-rumen wall muscles, the size and specific gravity of forage particles, selective regurgitation of large particles, and selective particle escape through the reticulo-omasal orifice (Lechner-Doll, Kaske & Engelhardt, 1991). The creation of a rumen mat is characteristic for grazers for which natural diet contain large amounts of fibrous material (Demment & Van Soest, 1985, chapter 15). This floating raft mainly consists of large particles from newly ingested forage, likely of being regurgitated and exposed to further mastication. Aided by reticulo-rumen wall contractions, the remaining reticulo-rumen content is filtered through the mat potentially causing additional particles to be entrapped; despite a smaller size and relatively higher specific gravity. This efficient mechanism of particle retention related to the stratification of rumen content is thought to be responsible for the minor influence of body mass on faecal particle size distribution among grazers (Clauss *et al*., 2002). The mechanism involved in selective retention of particles in browsers and mixed-feeders is largely unexplained (Clauss *et al*., 2001; Clauss *et al*., 2002). Ingestion of less fibrous material mixed with copious saliva, makes the reticulo-rumen content of browsers and mixed-

feeders generally more viscous and more homogenous. In addition, weaker reticulo-rumen wall muscles generate less mixing. Selective particle retention among browsers and mixed-feeders does therefore seem more dependent on functional properties of forage particles alone, underlining that the efficiency of mastication may be of particular importance (but see Lechner-Doll *et al*., 1991).

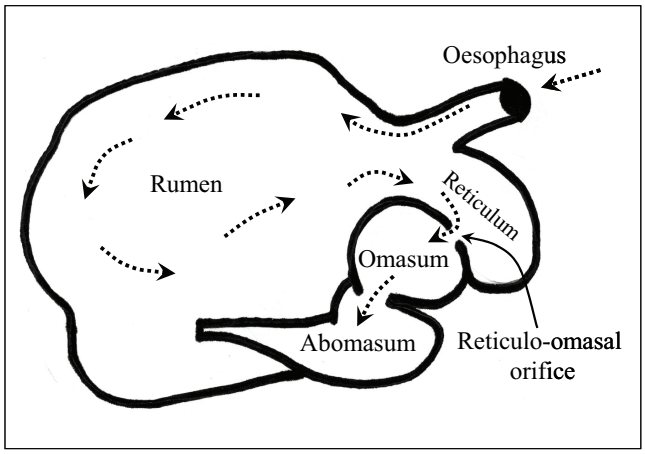

Figure 2. Functional division of the ruminant stomach. Dashed lines indicate digestive flow. Arrow with solid line gives the location of the reticulo-omasal orifice (Redrawn after various authors.)

ALTERATIONS OF RETICULO-RUMEN DYNAMICS IN RESPONSE TO FORAGE QUALITY

Ruminants experiencing seasonal variation in forage quality or abundance exhibit alterations both in rates of forage intake and passage, as well as in digestive tract morphology and proportions. These changes are of major importance to digestion efficiency and energy yield. The digesta normally occupies only a proportion of the total reticulo-rumen volume (Hofmann & Nygren, 1992), the rest being filled by gas and liquid. For grazers in particular, degree of filling increases with ingestion rate and forage fibre content (Van Soest, 1994). It is commonly accepted within the field of ruminant physiology that rumen filling is determined by physical characteristics of

the feed, which also affects digesta passage from the reticulo-rumen (Conrad, 1966). Increased filling is equivalent to increased reticulo-rumen retention time allowing longer exposure of forage particles to rumen microflora, and subsequently leading to a more complete digestion (Demment & Van Soest, 1985; Lechner-Doll *et al*., 1991; Hummel *et al*., 2006). The actual mechanism behind this prolonged retention time is most likely directly linked to the physicochemical particle properties, and the longer time needed for forage particles to attain the properties coinciding with the criteria for reticulo-omasal orifice passage.

A morphological change of great influence to nutrient absorption is the alteration in rumen wall papillation. The presence of mucosal papillae increases the rumen wall surface. Both the extent of papillation and the alterations in reticulo-rumen filling are closely related to forage quality. For ruminants, where digestive efficiency greatly depends upon microbial fermentation, an increase in average forage particle size – as a consequence of tooth wear related reduction in mastication efficiency – will equal a reduction in forage quality. Unless compensatory mechanisms enable adequate buffering of this negative effect of dental wear, the ultimate consequence will be reduced net energy gain per unit time. The functional relevance of tooth wear in ruminants, and the significance of potential compensatory mechanisms has to date been little explored. This was the motivation for the study synthesized in Paper II.

FEEDING TYPE CLASSIFICATION: THE BROWSER-GRAZER CONTINUUM

Plant foods exhibit considerable variation in nutritional content, physical structure and chemical composition (Van Soest, 1994). Among these features, forage fibre content has been pointed out as the most influential one with respect to physiological and morphological adaptations within the ruminant digestive system (Van Soest, 1994). In general monocotyledons (e.g., willow, herbs, forbs and sedges) – in a dietary context usually referred to as browse – containing less fibre than dicotyledons (mainly grasses).

Ruminants differ in their dietary preferences, in their ability to discriminate between food items, and in

their capacity to digest and utilize various diets. These differences are intimately associated with morphological characteristics of the digestive tract (see Perez-Barberia et al. [2004] for an in depth discussion). Based on behavioural observations, Bell (1971) and Jarman (1974) were the first ones to acknowledge the significance of these adaptations for diet selection and niche separation. Later, the classification of feeding-types was explicitly elucidated based on morphophysiological criteria (Hofmann & Stewart, 1972; Hofmann, 1973; Hofmann, 1989). The most commonly referred differences between browsers, mixed-feeders and grazers are related to capacity of fibre digestion and ability to discriminate between food items. The feeding strategy of browsers rely on satisfying their energy need through ingesting relatively low amounts of food of high quality (low fibrous content), implying a generally more choosy feeding strategy than grazers. The mixed-feeders exhibit digestive characteristics and feeding strategies overlapping the two other groups. This implies that they are more capable of switching strategy according to seasonal variation in forage quality and abundance. A number of other features highlighting the difference between feeding types are listed in Fig. 3. The relevance of dietary preference to this study is through its effect on food properties and ultimately expected consequence on tooth wear (Paper IV).

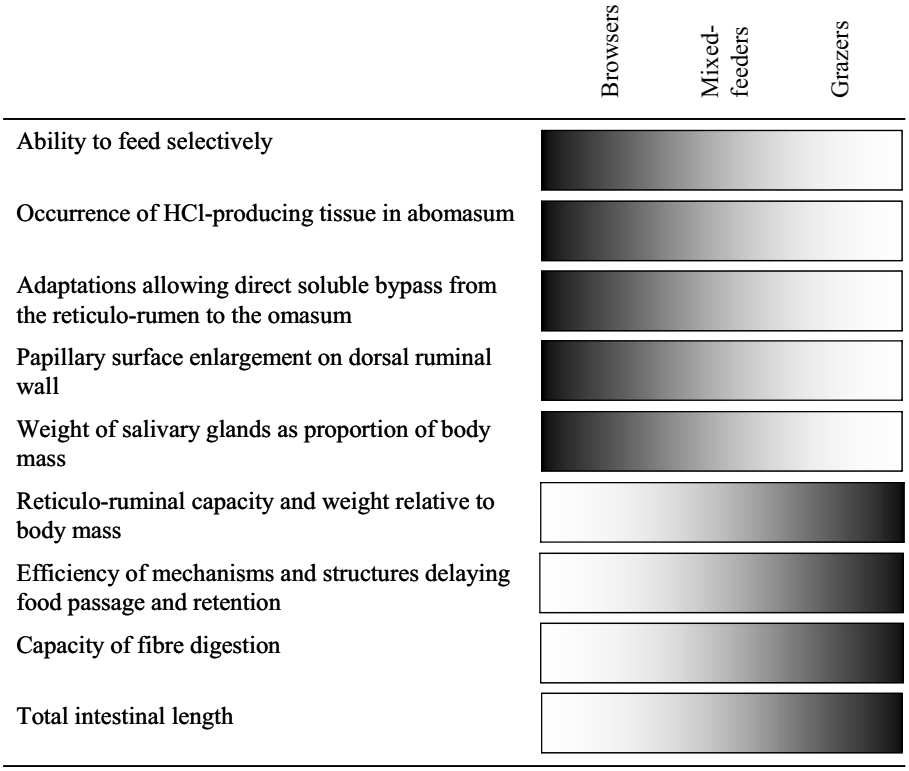

Figure 3. A list of characteristics changing along the browser-grazer continuum. The degree of shading is a relative indication of ability, proportion or occurrence of various characteristics related to digestive morphology. Darker shading indicates superior ability, higher proportions and occurrences, or longer measures.

MATERIAL AND METHODS

Data on four different deer species were used to investigate the questions raised: reindeer *Rangifer tarandus* L., moose *Alces alces* L., red deer, and roe deer *Capreolus capreolus* L. The species and their respective study systems were chosen both due to their biological characteristics and also based on the feasibility to achieve the relevant data material. The following sections will provide brief presentations of the study systems with special attention on characteristics of interest for the approaches of this thesis.

SVALBARD REINDEER – LIVING AT THE POLAR FRONTIER

Svalbard reindeer, *Rangifer tarandus platyrhynchus* Vrolik, is the northernmost living cervid, and the only large herbivore inhabiting the archipelago of Svalbard. The earliest indications of its presence is the finding of reindeer droppings in peat cores dated to before 7000 years BP (Van der Knaap, 1986). Based on genetic data, both an eastern and a western colonization route have been promoted as plausible alternatives (Røed *et al*., 1986; Gravlund *et al*., 1998; Flagstad & Røed, 2003), collectively implying that colonization took place during the retreat of the ice sheet after the last glacial period 5-10 000 years BC.

Svalbard is characterized as an arctic desert with extreme seasonality, severe winters, and only approximately three months with average temperatures above zero. The Svalbard reindeer is consequently adapted to survive under harsh climatic conditions and on very limited food supplies during most of the year. A number of external morphological characteristics distinguish the Svalbard reindeer from its relatives, the most striking being a small body, short appendages and long fur. Apart from additional internal characteristics related to forage digestion (Sørmo *et al*., 1999; Mathiesen, 1999), the most distinctive characteristic of Svalbard reindeer is their extraordinary ability of fat deposition. These fat storages may constitute as much as 40% of late autumn dressed weight (Reimers & Ringberg, 1983) and 25% of the total winter energy requirements (Tyler, 1987).

Despite the minor influence from predation and harvesting, Svalbard reindeer populations fluctuate widely, mainly as a consequence of stochastic climatic incidents and density dependent food limitations (Solberg *et al*., 2001; Aanes *et al*., 2003; Kohler & Aanes, 2004; Chan *et al*., 2005). The relative simplicity of the Arctic ecosystem makes Svalbard reindeer an interesting case, when studying mechanisms related individual life-history, as well as general population dynamics. From the morphological and physiological adaptations described, and also based on the inferred conclusions in Van der Wal and co-workers (2000), food availability (and not food quality) is a limiting factor to reindeer performance in Svalbard. Another factor, suggested to limit life span, is tooth wear (Tyler, 1987). These

are all ideal features for exploring mechanisms of primary importance to food utilization, and the potential consequences of variation within these properties.

MOOSE – THE LARGEST CONTEMPORARY CERVID

The main distribution range for moose falls within the circumpolar boreal vegetation zone. Adaptations like large body size, tolerance to low temperatures, substantial flexibility in digestive processes, and long legs, are some of the features enabling moose to overcome the large seasonal variations in temperatures and forage quality, as well as periods of deep snow cover.

The Norwegian moose represents the westernmost population within the distribution range of the European moose. Despite its long presence (Schmölcke & Zachos, 2005), population sizes have most likely never exceeded the numbers experienced during the last few decades. With its distribution range covering the greater part of Norway (exceptions only for the southwestern areas) the moose populations cover substantial gradients in environmental conditions[2]. Density dependent reduction in body mass and reproduction has also been documented in several areas (Solberg *et al*., 1999; Solberg *et al*., 2006). The most likely causal link between population density and animal performance, is that as density increases in a given area, ungulates often eat a lower quality diet (Fowler, 1987; Freeland & Choquenot, 1990). To maintain energy gain, animals are expected either to i) increase ingestion and passage rate, or ii) increase processing investment in terms of mastication. In either case, increased tooth wear rates are expected.

The moose is hunted throughout its entire distribution range. From selected regions hunter-provided information and material have been collected by the National Monitoring Program for cervids. This material is used to extract data on demography and production. Data from six of these regions – covering a north-south gradient (Fig. 4; for more details about study sites see Paper IV) – was used to investigate if spatial variation in environmental factors cause intraspecific variation in tooth

[2] For distribution maps and harvest numbers see: www.ssb.no/english/subjects/10/04/10/elgjakt_en/

wear.

If food quality is expected to induce differences in tooth wear rates within species, even larger differences would be expected between species showing consistent quality differences in their preferred diets (Janis, 1988; Perez-Barberia *et al*., 2004). This was investigated further by combining the existing data material on moose (a browser) with a similar data set from red deer (a mixed-feeder).

RED DEER – A FLEXIBLE FORAGER ON ITS DISTRIBUTION BORDERS

Red deer is one of the most widespread and best studied deer species with indigenous populations mainly being found in the temperate zones of Eurasia and North-America. The Norwegian population represents the northernmost distribution range of red deer in Europe (Koubek & Zima, 1999). There is common agreement about the present population being the descendants from ancestors surviving in ice-free refuges during the last glacial (Langvatn, 1999).

Population size and distribution range of Norwegian red deer has never been greater than at present[3]. Still, the majority of the population is found in the traditional core areas on the coastal parts of southwestern and middle Norway. The main vegetation characteristics of its range fall into the boreonemoral classification with only few local exceptions (Abrahamsen *et al*., 1977). Despite this, considerable variations in environmental conditions occur largely as a consequence of altitude, latitude and distance to coast (Mysterud *et al*., 2001a; Pettorelli *et al*., 2005).

Although harsh winter conditions may cause severe die-offs particularly among calves (Loison, Langvatn & Solberg, 1999), the main cause of mortality among red deer is hunting. Like for the moose, red deer is harvested through most of its distribution range, and hunters from selected regions collect information and material for the National Monitoring Program for cervids. Habitat quality and deer densities varies within these regions (Mysterud *et al*., 2001b), and density dependent effects on body mass (Mysterud *et al*., 2001b) as well as timing and synchrony of ovulation (Langvatn *et al*., 2004) has been

[3] For distribution maps and harvest numbers see: www.ssb.no/english/subjects/10/04/10/hjortejakt_en/

demonstrated. Data from four of these regions (Fig. 4), representing a north-south gradient, was used to investigate intraspecific patterns in tooth wear as a consequence of variation in environmental conditions. The red deer data was later combined with the moose data for analyses of interspecific patterns in tooth wear.

ROE DEER – THE SMALLEST NATIVE RUMINANT IN EUROPE

During the post-glacial period (14 000-10 000 years BP), roe deer colonized large parts of Europe at the same time as the human population expanded, and many larger mammals went extinct. High fecundity and large ability of rapid dispersion make roe deer a superior colonizer. Together with its adaptation to human presence through exploitation of cultural landscapes, these features are likely the main causes for its success (Andersen, Duncan & Linnell, 1998).

Unlike most other cervids, the roe deer is approximately monomorphic with bucks about 10% larger than does. Another distinctive characteristic is that females are monoestrus (meaning that they do not recycle if not fertilized) (Short & Hay, 1966; Aitken, 1974), and that the rutting season and fertilization takes place in late summer, only 1.5-2 months post parturition. After fertilization the blastocyst go through a few divisions before entering a five month period of embryonic diapause (delayed implantation). By shifting the timing of the rut to a period with abundant availability of high quality forage, the negative consequence (in terms of increased mortality) of the exhausting territorial defence is minimized for rutting bucks.

Today, roe deer is widely distributed and found in most parts of temperate Europe (Andersen *et al*., 1998). Within this large distribution range, substantial variation in environmental conditions has generated significant variation in several life-history traits (Gaillard *et al*., 1993; Gaillard *et al*., 1997; Andersen *et al*., 1998; Kjellander, Gaillard & Hewison, 2006). The roe deer material used in this study originate from two fenced (for more than 30 years) populations inhabiting habitats of contrasting quality. Based on knowledge about roe deer habitat requirements, the Trois Fontaines reserve in northern France (13.6 km^2) has been characterized

as a high quality habitat, while the Chizé reserve (26.1 km^2) in southwestern France has been characterized as a low quality habitat (Pettorelli *et al*., 2006). Population density in both sites has been managed through population control programs. Based on information from capture-mark-recapture data, animals from Chizé have been found to be smaller and less productive, but to live longer than animals inhabiting Trois Fontaines (Gaillard *et al*., 1993; Gaillard *et al*., 1997; Gaillard *et al*., 2003; Pettorelli *et al*., 2006).

Intraspecific variation in habitat quality is expected to cause differences in tooth wear rates. As a result, teeth durability may be expected to represent limitations to animal life-history in some populations but not in others. The two French study sites provided material that enabled this hypothesis to be investigated.

Table 1. Some key life-history characteristics for the study species, and references to the papers in which the species occur.

	Live adult body mass (♂/♀)	Offspring per reproductive event	Age at maturation[1]	Maximum lifespan (♂/♀)	Feeding-type	In thesis
Svalbard reindeer	90-120 / 60-70	1	2	16 / 17	Mixed-feeder[2]	Paper I & II
Moose, Norway	400-540 / 340-380	1-2	1-2	21 / 21	Browser	Paper IV
Red deer, Norway	160-200 / 100-150	1	1-2	18 / 26	Mixed-feeder	Paper IV
Roe deer, France	22-30 / 20-27	1-2	1	14 / 18	Browser	Paper III

[1]: Age when >50% of the females are expected to ovulate.
[2]: Hold characteristics of both browsers and mixed-feeders.

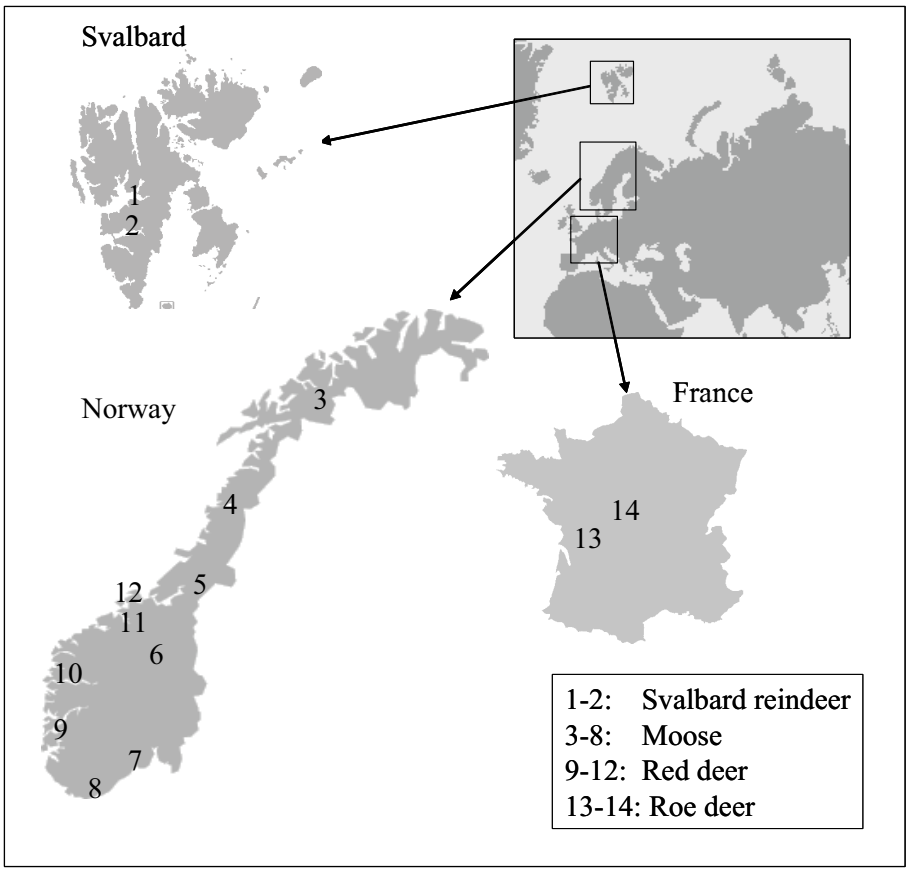

Figure 4. The distribution of study sites. Svalbard reindeer, 1: Sassendalen, 2: Colesdalen/Reindalen; moose, 3: Troms, 4: Nordland, 5: Nord-Trøndelag, 6: Oppland, 7: Vestfold/Buskerud/Telemark, 8: Vest-Agder; red deer, 9: Hordaland/Rogaland, 10: Sogn og Fjordane, 11: Møre og Romsdal/Sør-Trøndelag, 12: Hitra; roe deer, 13: Chizé, 14: Trois Fontaines.

MEASURING TEETH

In Paper III and IV height of the first molar (M_1) and the second incisor (I_2; Paper III only) was measured by using a digital calliper. The height of M_1 was measured as the perpendicular (relative to the jawbone) distance from the peak of the distobuccal cusp to the enamel/cementum line (Loe *et al*., 2003). The height of I_2 was measured as the height from the tooth crown to the lower enamel boundary at the anterior middle of

the tooth. All measures were recorded with a precision of 0.01 mm.

The main problem with using tooth height as a proxy for wear-related change in functionality is the assumption of their relationship. A given amount of wear will most likely have rather different consequences for small vs. large animals, and depending on whether the species studied possess brachyodont or hypsodont teeth (molars). Further, a tooth height reduction of, e.g., 1 mm, may also be expected to have different functional effect, depending on whether the teeth are newly erupted or nearly worn down. Though measures of molar height most likely represents good proxies for the overall consequences of wear, more detailed measures of occlusal topography will yield better insight into the actual wear-related alterations of functional tooth properties.

Recent developments in computerised scanning imaging technologies combined with powerful image analysis software have made it possible to represent and interpret three-dimensional objects (such as teeth) (Evans, Harper & Sanson, 2001; Scott *et al*., 2005). In Paper I, I employed a novel method developed for collecting accurate, high resolution data on topographic variation. The occlusal surface of M_1 was digitized using structured light projection; which is a triangulation based optical 3D shape measurement technique (Sansoni, Carocci & Rodella, 1999). A data projector was used to illuminate the object under measurement with a sequence of light patterns. The object was observed with a video camera placed at an angle with regard to the direction of projection. In each pixel of the camera the observed intensities in the sequence make up an optical "code" that can be processed to yield the height of the object. A telecentric camera objective ensured that the influence of perspective was minimal and lateral pixel size was determined with standard camera calibration techniques. The field of view was set to approximately 40x30 mm with a lateral resolution of 0.055 mm. Calibrated height range was approximately 24 mm and the height accuracy 0.01 mm.

The shininess and transparency of enamel may cause considerable measuring errors when using structured light projection. To minimize this problem, the occlusal surface was sprayed with a developer producing a fine

and even coating of the surface examined. Measurements, resulting in a matrix of height values, were controlled by the HoloVision software (developed at SINTEF ICT, Department of Optical Measurement Systems and Data Analysis) before read in to Matlab® for further processing. This direct link between the scanning procedure and analytical software allowed immediate quality assurance of all scans.

RESULTS AND DISCUSSION

THE CONSEQUENCES OF AGE AND BODY GROWTH PATTERNS ON TOOTH WEAR AND ITS IMPLICATIONS ON FORAGE MASTICATION (PAPER I)

Dental functionality and durability represent key factors affecting forage utilization in all large herbivores. In this study, we used material from 117 Svalbard reindeer females of known age and body mass to assess particle size distribution in rumen content. The animals were harvested from two populations. Structured light projection was used to extract information about tooth height and molar occlusal topography (tooth wear) from 48 individuals. We then explored the relationships between tooth wear, particle size in rumen, age and body mass in female Svalbard reindeer. The following hypotheses were derived and tested:

H1: If tooth wear is the constraining factor for rumen particle size, and if tooth wear is mainly a function of age, average particle size in rumen should increase with age. There should be no residual effect of age on rumen particle size after adjusting for tooth wear and body mass.

H2: From allometric relations it is known that larger individuals can survive on a lower quality diet. We therefore predicted larger particle sizes with increasing body mass, irrespective of age and wear.

H3: If there is a trade-off between body growth and tooth wear, teeth of heavier animals should be more worn than lighter animals of the same age.

We found that the proportion of small particles (<1.0 mm) decreased

rapidly with increasing age (consistent with H1). There was no consistent support for an overall effect of body mass on rumen particle size (rejecting H2), but heavier animals within younger age classes had more worn teeth than lighter ones (supporting H3).

Apart from these main results, we found significant difference in rumen particle size distribution between the two study populations and between years even when controlling for several relevant covariates. These results suggest that additional factors (e.g., other environmental factors) influence particle size. Food quality, measured as fibre content, is well known to affect digestive processes and increase reticulo-rumen retention time (Van Soest, 1994). Subsequently, increased retention time may cause ingested particles to be masticated more thoroughly. Hypothetically, access to high quality food resources may be related to age – potentially as a consequence of learning or dominance. As an indication of food quality, information on diet composition was revealed through a point-identification method using subsamples of rumen content (n=66) (Gaare, Sorensen & White, 1977). Diet composition was not found to influence the age-related effect on rumen particle size.

Together with tooth height, variation in occlusal topography decreased with age. This was followed by a corresponding decrease in average proportions of small rumen particles, indicative of reduced mastication efficiency. Despite that heavier individuals up to ≈ 5 years of age showed more extensive tooth wear than lighter ones, a close to isometric relationship between particle size and body mass suggested that heavier animals partly compensated reduced tooth efficiency by chewing more. This result implies that available time for processing becomes a limiting factor at advancing age. The index for occlusal topographic variation, was a marginally better predictor for rumen particle size distribution, than both age and tooth height. On the other hand, their approximately equal performance shows that both age and tooth height may be used as trustworthy proxies for tooth wear – at least for Svalbard reindeer.

This study provides the first evidence of a trade-off between fast early growth, and wear of a senescence related trait (structure and height of molars) in a

wild ruminant. Fossil evidence suggests that increased molar height evolved as an adaptation for wear tolerance in dry ecosystems with sparse vegetation (Fortelius et al., 2002); not unlike the arctic deserts of Svalbard. This suggests that the foraging conditions experienced by the Svalbard reindeer might represent a selection pressure for higher teeth.

INCREASED RETICULO-RUMEN DIMENSION AND FILL WITH ADVANCING AGE IN SVALBARD REINDEER: CAUSES AND CONSEQUENCES (PAPER II)

Age-related tooth wear alters the occlusal surface topography in predictable ways, causing gradual loss of functionality. Unless compensated through increased chewing investment (or other mechanisms), this will lead to increased average rumen particle size, increased retention time and reduced energy gain. This suggests that occurrence of directional changes in digestive processes may be expected as animals age. Reticulo-rumen dimension has large influence on the capacity to digest forage of low quality (Van Soest, 1994). An average increase in forage particle size presented to the rumen microflora equals the effect of a general food quality reduction. As an adaptation to these predictable alterations in food particle properties, a permanent increase in reticulo-rumen volume would represent a long-lasting compensating mechanism.

Increased fill of reticulo-rumen is equivalent to increased rumen retention time (Van Soest, 1994). This allows longer exposure of forage particles to rumen microflora, and subsequently leading to a more complete digestion (Demment & Van Soest, 1985; Lechner-Doll *et al*., 1991; Hummel *et al*., 2006).

Energy intake in Svalbard reindeer is suggested to be limited by forage abundance (Van der Wal *et al*., 2000). A compensation for reduced forage mastication efficiency through increased forage ingestion is therefore an unlikely alternative. In principle, most mechanisms related to digestive processes in ruminants may (through alterations in capacity or activity) compensate for lowered forage quality. The extent to which they can be altered, are on the other hand limited by mechanical (body cavity and competition with other internal organs/tissue) constraints, and most likely also by

evolutionary history.

Using data from 49 adult Svalbard reindeer females, we investigated whether mass of reticulo-rumen content (indicative of increased rumen retention times), reticulo-rumen tissue (indicative of rumen volume), and amount of back fat showed age-related changes. The hypotheses we tested were:

H1: To actively compensate for the gradual reduction in mastication efficiency and increased particle size (having similar effects as reduced forage quality), we predict that the weight of the reticulo-rumen will increase with age.

H2: As a consequence of age-related deterioration of mastication efficiency, alterations of forage particle properties are expected to cause increased reticulo-rumen filling with increasing animal age.

H3: Despite the potential effect from passive (H1) and active (H2) compensating mechanisms, we expect that energy gain is reduced with age. We therefore predict that energy storages (amounts of back fat) will decrease with advancing age.

We found that the mass of reticulo-rumen content and tissue increased, while amount of back fat decreased with advancing age (supporting all our hypotheses). The increase of reticulo-rumen tissue, indicative of increased reticulo-rumen volume, suggest that physiological alterations occur in response to decreased mastication efficiency, similar to changes known to occur when adapting to seasonal reduction in plant quality. These changes cause a permanent increase in digestive capacity. Obviously, the amount of reticulo-rumen content is expected to increase purely as a consequence of the enlarged chamber dimensions. The importance of chamber enlargement vs. alterations of physicochemical particle properties can not be definitely established from our data. We tried to estimate the expected increase in reticulo-rumen content as a response to increased reticulo-rumen tissue (corrected for other factors). Though the parameter estimate was positive, it was not significant emphasising the need for more data to establish this relationship with certainty. However, the slope for age-related increase in reticulo-rumen content weight

was steeper than for tissue weight, suggesting that the increase in volume may not fully explain the pattern of increased reticulo-rumen content. We argue that both these mechanisms potentially cause prolonged exposure of ingesta to rumen microflora, subsequently leading to (at least partly) maintenance of digestion efficiency.

Amount of back fat still decreased with age, suggesting that alterations in digestion related processes were not sufficient to compensate for reduced mastication efficiency in Svalbard reindeer.

Our findings on Svalbard reindeer demonstrate that reticulo-rumen filling increase with age, suggesting that increased tooth wear and poorer mastication causes increased retention times. Increased rumen retention time is regarded a central mechanism to increase energy uptake from low quality forage, but since time is lost in this process, it cannot alone fully compensate for the reduced digestion efficiency due to tooth wear. Hence, our results showing an age-related increase in reticulo-rumen tissue mass present one further link between foraging, digestive processes and life-history patterns.

TOOTH WEAR AND LIFESPAN (PAPER III)

The role of tooth wear as a proximate cause of senescence in ruminants has recently been highlighted (Tyler, 1987; Gaillard *et al*., 1993; Loe *et al*., 2003; Carranza *et al*., 2004). There are two competing hypotheses to explain variation in tooth height and wear; the diet quality hypothesis predicting increased wear in low quality habitats, and the life-history hypothesis predicting molar height to be related to expected longevity. So far, these hypotheses, which are not mutually exclusive, have mainly been used to explain variation in tooth wear and height between the sexes of highly polygynous species. No study has related between-population differences in tooth wear and height to differences in life-history variables. We aimed to test both of these hypotheses, and compared tooth height and wear from roe deer of known age from two contrasting populations of roe deer in France; Trois Fontaines (TF) with good habitat and shorter animal life expectancy and Chizé (CH) with poor habitat and longer animal life expectancy.

There was no difference in the rate of tooth wear between the populations, leading to rejection of the diet quality hypothesis. Due to the fairly limited sample size, and the fact that wear may not be linear with age (Loe *et al*., 2003), it is somewhat premature to reject a role of habitat quality even for the focal populations. Despite their smaller body size, initial molar height for animals from CH was larger than for animals from TF (both absolute and relative to body size). This provides the first evidence that variation in longevity between populations can lead to differences in molar height within a species.

The evolutionary processes related both to life-history and to diet quality may work in the same direction on molar size, and may well be linked. The longer lifespan expectancy for animals inhabiting an inferior habitat could be explained through stress-responsive survival and its relationship with "caloric restriction" (Sinclair, 2005). Caloric restriction has been widely accepted as a cause of extended longevity in numerous species (Masoro, 2000; Sinclair, 2005). The evolutionary basis of this relies on the presence of a potential future reproductive gain. Since the effects of dental senescence is expected to be most pronounced in mammals living in seasonal habitats (King *et al*., 2005), our linkage between lifespan and teeth endurance is in correspondence with evolutionary predictions.

THE ECOLOGY AND EVOLUTION OF TOOTH WEAR (PAPER IV)

Tooth wear is caused by processing of food, and the characteristics of the food ingested is related both to the evolutionary history of the animals (Perez-Barberia & Gordon, 1999) as well as current ecological conditions (Choquenot, 1991). Differences in body size and dietary preferences have formed functional traits of ruminant digestive system (Demment & Van Soest, 1985; Hofmann, 1989), including tooth design (Janis, 1988; Archer & Sanson, 2002). Grazers and mixed-feeders eat a more fibrous diet than browsers (Perez-Barberia *et al*., 2004), which arguably increase tooth wear. Solounias et al. (1994) suggested that tooth wear was positively correlated with body mass across feeding-types. Theoretical deductions have on the other hand questioned such a relationship (Fortelius,

1987). For species with large distribution ranges, different populations may be exposed to very different ecological factors affecting diet and thus tooth wear rates (Skogland, 1988; Kojola *et al*., 1998; Loison *et al*., 2001; Nussey *et al*., 2007). Still, quantification of how both contemporary ecological conditions as well as evolutionary history (related to feeding-type) affect tooth wear patterns is lacking.

In this study, we compared inter- and intraspecific rates of both incisor and molar wear in one large browser (moose, six populations, n=1063) and one mixed-feeder (red deer, four populations, n=5519) covering the main distribution range of each species in Norway. We tested the following hypotheses:

H1: If feeding-type is the most important determinant of diet and subsequently tooth wear, a faster overall molar wear is expected in the mixed-feeder compared to the browser.

H2: Since the selective feeding strategy of browsers may be associated with higher biting rates and less chewing, the browser is expected wear incisors faster than the mixed-feeder.

H3: If body size is the most important determinant for tooth wear, the larger moose should wear teeth faster than red deer.

H4: If ecological conditions are more important for wear rates than the differences in evolutionary history, variation in tooth wear between populations is expected to be larger than variation between species.

Our analyses revealed that the mixed-feeding red deer wore teeth faster than the larger and browsing moose (both on an absolute and relative scale). This suggests that feeding-type was more important for tooth wear patterns than body size. The conclusions regarding feeding-type and tooth wear rates in Solounias et al. (1994), was confounded by the fact that the only browser included in the study also happened to be the smallest species. The wear rates reported here for moose, our largest contemporary browsing cervid, thus provide the first evidence of lower molar wear rates in a browser irrespective of body mass (though certainly, this is not a full comparative study). This result is in agreement with the expectations both

related to dietary fibre content, and from the previous finding of generally more hypsodont teeth (indicating a more intensive wear) among mixed-feeders than among browsers (Janis, 1988).

Both species wore incisors at a lower rate than molars. Contrary to our prediction, also incisor wear rate was found to be highest in the mixed-feeder. This indicates that incisor (as well as molar) wear is primarily related to forage characteristics and amount of forage ingested, rather than to a predicted difference in foraging behaviour. On the other hand, no close correspondence between incisor and molar wear rates could be detected at the population level for neither red deer nor moose.

Within their large distribution ranges, the two species experience substantial ecological variation, and wear rates showed considerable variation between populations (more evident in red deer than in moose). Still, the consistency of species-specific molar wear patterns suggests that subsampling within species is a minor source of variation in comparative studies.

At last, we also tested whether spatial variation in wear could be related to coarse scale population density (cf. Nussey *et al*., 2007), and whether this potential density dependency differed between species. Density dependency was only consistent for molar wear rates in male red deer (the male material for moose was too limited to conclude). The spatial variation in population density was unable to account for all of the spatial variation in tooth wear. This may suggest that population density by itself is of less importance compared to spatial variation in habitat quality.

Our findings are consistent with the view that evolutionary history is responsible for the main patterns of tooth wear rates between-species, and that within-species variation, due to current ecological conditions, are less explicit – at least within the distribution ranges in our study.

CONCLUDING REMARKS

Well functioning teeth are essential for digestive processes in ruminants, and their persistent functionality and durability are of major importance to animal performance. Teeth wear as a result of extensive use over time and the abrasive properties of plant foods. With increasing age, animals may therefore

experience reduced mastication efficiency potentially limiting life-history strategies such as body growth and life span. This thesis presents some of the first studies that explicitly quantify important patterns (Paper I, III & IV) and causes (Paper I) of tooth wear and tooth height in wild cervids. It also presents rare evidence of the relationship between tooth wear and life-history (Paper III), as well as the consequences for digestive processes (reticulo-rumen particle size, rumen retention time) and subsequently fat deposition or growth (Paper I & II).

Previous studies have revealed the likely evolutionary driving forces for the interspecific variation in teeth characteristics observed in large herbivores (Fortelius, 1985; Janis, 1988; Fortelius *et al*., 2002). Differing tooth morphologies have arisen from the different demands related to processing of diverse diets (Janis & Fortelius, 1988; Janis, 1988). Despite their high degree of specialization and resistance to wear, teeth deteriorate as a result of use. Despite this fact, the actual consequences have to a little extent been quantified in wild, large herbivores. As predicted, increasing wear in Svalbard reindeer led to increased particle size in the reticulo-rumen likely due to reduced mastication efficiency (Paper I). This in turn led to increased reticulo-rumen filling and enlarged reticulo-rumen volume (Paper II). Both of these changes arguably led to increased retention time and digestive capacity, likely able to (at least partially) compensate the negative consequences from tooth wear (Paper II). Despite these changes, a reduced energy uptake was revealed through a markedly reduced amount of fat as animals aged (Paper II). This provides an improved mechanistic understanding of the processes leading to a decrease in performance as animals age. Such insight is important, as it enables a better understanding of age-specific survival and why older animals are particularly prone to die in periods of harsh climate (Gaillard, Festa-Bianchet & Yoccoz, 1998; Gaillard *et al*., 2000). Such an understanding has proven necessary to successfully predict the population dynamics of ungulate populations (Coulson *et al*., 2001).

Knowing that tooth wear has consequences for energy gain as animals age, patterns of wear can shed light on constraints for the life-history. Benefiting from extensive data sets on red deer and moose, I was able to investigate both

inter- and intraspecific variation in tooth wear patterns related to feeding-type (dietary preferences) and variation in environmental conditions (Paper IV). In addition to strengthen the generality of previous studies (Solounias, Fortelius & Freeman, 1994), our results clearly demonstrated the influence of spatial variation in ecological conditions. Interestingly, this was more important for the mixed-feeder, suggesting that variation in tooth wear will be a more variable and important constraint for the life-history in mixed-feeders compared to browsers. For two French populations of roe deer (Paper III), significant differences in initial molar height were linked to differences in expected life span, and not to differences in habitat quality. This lack of influence from spatial variation in environmental conditions in the browsing roe deer is consistent with the results from moose. Clearly, data from more species (both browsers and mixed-feeders) are needed to assess the generality of these patterns. Still, their life span expectancy and their performance are indisputable linked to their environment.

Tooth design is continuously shaped by a dynamic interplay between environmental conditions as well as the demands related to animal life-history, in particular longevity. If tooth height was a limitation to animal lifespan, we would expect evolution working to increase tooth height (as found in Paper III). It was therefore particularly interesting to find strong indications of a selection pressure towards increased tooth height in Svalbard reindeer, even after more than 5 000 years of presence on the archipelago (Paper I). The reason why teeth still seem to be a factor under selection, could be due to the large influence from stochastic environmental effects (icing events) on survival (Solberg *et al*., 2001; Aanes *et al*., 2003; Kohler & Aanes, 2004). Depending on the strength of heritability, such events may disrupt a directional evolution (Kruuk *et al*., 2002). It also suggests that other features or strategies are more important to animal life-history, and thus exposed to an even larger selection pressure. To attain closer understanding of the consequences tooth wear has for individual fitness, longitudinal data with detailed information on individual performance would be rewarding. This would allow further evaluation of selection pressure and the performance of individuals with

differing life-histories (Coulson *et al*., 2006).

Future work should aim at understanding the constraints of digestive processes in ruminants, how they are affected by age-related alterations in physical properties (e.g., teeth), and ultimately the traceability of these changes into animal performance. Longitudinal data with repeated tooth wear measurements from identified animals over a given period of time (preferable their lifetime), would improve our ability to quantify the costs related to important life-history events such as reproduction, and provide information about potential annual variation in wear. Attaining such information from wild populations is time and resource demanding; and these challenges are yet to be overcome.

Acknowledgements
I am very grateful to Atle Mysterud, Rolf Langvatn, Nils Chr. Stenseth and Leif Egil Loe for constructive and valuable comments on previous drafts of this introduction.

REFERENCES

Aanes, R., Sæther, B.-E., Solberg, E. J., Aanes, S., Strand, O., & Øritsland, N. A. (2003). Synchrony in Svalbard reindeer population dynamics. *Canadian Journal of Zoology-Revue Canadienne de Zoologie* **81:** 103-110.

Abrahamsen, J., Jacobsen, N. K., Kalliola, R., Dahl, E., Wilborg, L., & Påhlsson, L. (1977). Naturgeografisk regioninndeling av Norden. *Nordiske Utredninger* **B 34:** 1-135.

Aitken, R. J. (1974). Delayed implantation in roe deer (*Capreolus capreolus*). *Journal of Reproduction and Fertility* **39:** 225-233.

Andersen, R., Duncan, P., & Linnell, J. D. C. (1998). *The European roe deer: the biology of success*. Oslo: Scandinavian University Press.

Archer, D. & Sanson, G. (2002). Form and function of the selenodont molar in southern African ruminants in relation to their feeding habits. *Journal of Zoology* **257:** 13-26.

Bell, R. H. V. (1971). Grazing ecosystem in Serengeti. *Scientific American* **225:** 86-93.

Carranza, J., Alarcos, S., Sanchez-Prieto, C. B., Valencia, J., & Mateos, C. (2004). Disposable-soma senescence mediated by sexual selection in an ungulate. *Nature* **432:** 215-218.

Chan, K. S., Mysterud, A., Øritsland, N.

A., Severinsen, T., & Stenseth, N. C. (2005). Continuous and discrete extreme climatic events affecting the dynamics of a high-arctic reindeer population. *Oecologia* **145:** 556-563.

Choquenot, D. (1991). Density-dependent growth, body condition, and demography in feral donkeys - testing the food hypothesis. *Ecology* **72:** 805-813.

Clauss, M. & Hummel, J. (2005). The digestive performance of mammalian herbivores: why big may not be that much better. *Mammal Review* **35:** 174-187.

Clauss, M., Lechner-Doll, M., Behrend, A., Lason, K., Lang, D., & Streich, W. J. (2001). Particle retention in the forestomach of a browsing ruminant, the roe deer (*Capreolus capreolus*). *Acta Theriologica* **46:** 103-107.

Clauss, M., Lechner-Doll, M., & Streich, W. J. (2002). Faecal particle size distribution in captive wild ruminants: an approach to the browser/grazer dichotomy from the other end. *Oecologia* **131:** 343-349.

Conrad, H. R. (1966). Symposium on factors influencing voluntary intake of herbage by ruminants - physiological and physical factors limiting feed intake. *Journal of Animal Science* **25:** 227-235.

Coulson, T., Benton, T. G., Lundberg, P., Dall, S. R. X., Kendall, B. E., & Gaillard, J. M. (2006). Estimating individual contributions to population growth: evolutionary fitness in ecological time. *Proceedings of the Royal Society B-Biological Sciences* **273:** 547-555.

Coulson, T., Catchpole, E. A., Albon, S. D., Morgan, B. J. T., Pemberton, J. M., Clutton-Brock, T. H., Crawley, M. J., & Grenfell, B. T. (2001). Age, sex, density, winter weather, and population crashes in Soay sheep. *Science* **292:** 1528-1531.

Demment, M. W. & Van Soest, P. J. (1985). A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. *American Naturalist* **125:** 641-672.

Ericsson, G. & Wallin, K. (2001). Age-specific moose (*Alces alces*) mortality in a predator-free environment: Evidence for senescence in females. *Ecoscience* **8:** 157-163.

Evans, A. R. (2005). Connecting morphology, function and tooth wear in microchiropterans. *Biological Journal of the Linnean Society* **85:** 81-96.

Evans, A. R., Harper, I. S., & Sanson, G. D. (2001). Confocal imaging, visualization and 3-D surface measurement of small mammalian teeth. *Journal of Microscopy-Oxford* **204:** 108-118.

Flagstad, O. & Røed, K. H. (2003). Refugial origins of reindeer (*Rangifer tarandus* L.) inferred from

mitochondrial DNA sequences. *Evolution* **57:** 658-670.

Fortelius, M. (1985). Ungulate cheek teeth: developmental, functional and evolutionary interrelations. *Acta Zoologica Fennica* **180:** 1-76.

Fortelius, M. (1987). A note on the scaling of dental wear. *Evolutionary Theory* **8:** 73-75.

Fortelius, M., Eronen, J., Jernvall, J., Liu, L. P., Pushkina, D., Rinne, J., Tesakov, A., Vislobokova, I., Zhang, Z. Q., & Zhou, L. P. (2002). Fossil mammals resolve regional patterns of Eurasian climate change over 20 million years. *Evolutionary Ecology Research* **4:** 1005-1016.

Fortelius, M. & Solounias, N. (2000). Functional characerization of ungulate molars using the abrasion-attrition wear gradient: a new method for reconstructing paleodiets. *American Museum Novitates* **3301:** 1-36.

Fowler, C. W. (1987). A review of density dependence in populations of large mammals. In *Current Mammalogy*: 401-441. Genoways, H. H. (Ed.). New York and London: Plenum Press.

Franz-Odendaal, T. A. & Kaiser, T. M. (2003). Differential mesowear in the maxillary and mandibular cheek dentition of some ruminants (Artiodactyla). *Annales Zoologici Fennici* **40:** 395-410.

Freeland, W. J. & Choquenot, D. (1990). Determinants of herbivore carrying capacity: plants, nutrients, and *Equus asinus* in northern Australia. *Ecology* **71:** 589-597.

Gaare, E., Sorensen, A., & White, R. G. (1977). Are rumen samples representative of diet. *Oikos* **29:** 390-395.

Gaillard, J. M., Boutin, J. M., Delorme, D., Van Laere, G., Duncan, P., & Lebreton, J. D. (1997). Early survival in roe deer: causes and consequences of cohort variation in two contrasted populations. *Oecologia* **112:** 502-513.

Gaillard, J. M., Delorme, D., Boutin, J. M., Van Laere, G., Boisaubert, B., & Pradel, R. (1993). Roe deer survival patterns - a comparative-analysis of contrasting populations. *Journal of Animal Ecology* **62:** 778-791.

Gaillard, J. M., Duncan, P., Delorme, D., Van Laere, G., Pettorelli, N., Maillard, D., & Rennesund, J. S. (2003). Effects of hurricane Lothar on the population dynamics of European roe deer. *Journal of Wildlife Management* **67:** 767-773.

Gaillard, J. M., Festa-Bianchet, M., & Yoccoz, N. G. (1998). Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends in Ecology & Evolution* **13:** 58-63.

Gaillard, J. M., Festa-Bianchet, M.,

Yoccoz, N. G., Loison, A., & Toïgo, C. (2000). Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics* **31:** 367-393.

Garrott, R. A., Eberhardt, L. L., Otton, J. K., White, P. J., & Chaffee, M. A. (2002). A geochemical trophic cascade in Yellowstone's geothermal environments. *Ecosystems* **5:** 659-666.

Gordon, I. J. & Illius, A. W. (1994). The functional-significance of the browser-grazer dichotomy in African ruminants. *Oecologia* **98:** 167-175.

Gravlund, P., Meldgaard, M., Paabo, S., & Arctander, P. (1998). Polyphyletic origin of the small-bodied, high-arctic subspecies of tundra reindeer (*Rangifer tarandus*). *Molecular Phylogenetics and Evolution* **10:** 151-159.

Hofmann, R. R. (1973). *The ruminant stomach: stomach structure and feeding habits of East African game ruminants*. Nairobi, Kenya: East African Literature Bureau.

Hofmann, R. R. (1989). Evolutionary steps of ecophysiological adaptation and diversification of ruminants - a comparative view of their digestive-system. *Oecologia* **78:** 443-457.

Hofmann, R. R. & Nygren, K. F. A. (1992). Morphophysiological specialization and adaptation of the moose digestive system (*Alces alces* L.). Proceedings 3rd International Moose Symposium, Syktyvkar, USSR. *Alces Suppl.* **1:** 91-100.

Hofmann, R. R. & Stewart, D. R. M. (1972). Grazer or browser: a classification based on the stomach structure and feeding habits of East African ruminants. *Mammalia* **36:** 226-240.

Hummel, J., Sudekum, K. H., Streich, W. J., & Clauss, M. (2006). Forage fermentation patterns and their implications for herbivore ingesta retention times. *Functional Ecology* **20:** 989-1002.

Janis, C. M. (1988). An estimation of tooth volume and hypsodonty indices in ungulate mammals, and the correlation of these factors with dietary preference. *Mémoires du Muséum National D'Histoire Naturelle (Series C)* **53:** 367-387.

Janis, C. M. & Fortelius, M. (1988). On the means whereby mammals achieve increased functional durability of their dentitions, with special reference to limiting factors. *Biological Reviews of the Cambridge Philosophical Society* **63:** 197-230.

Jarman, P. J. (1974). Social organization of antelope in relation to their ecology. *Behaviour* **48:** 215-267.

Jernvall, J. & Fortelius, M. (2002). Common mammals drive the evolutionary increase of hypsodonty in the Neogene. *Nature* **417:** 538-540.

King, S. J., Arrigo-Nelson, S. J., Pochron, S. T., Semprebon, G. M., Godfrey, L. R., Wright, P. C., & Jernvall, J. (2005). Dental senescence in a long-lived primate links infant survival to rainfall. *Proceedings of the National Academy of Sciences of the United States of America* **102:** 16579-16583.

Kjellander, P., Gaillard, J. M., & Hewison, A. J. M. (2006). Density-dependent responses of fawn cohort body mass in two contrasting roe deer populations. *Oecologia* **146:** 521-530.

Kohler, J. & Aanes, R. (2004). Effect of winter snow and ground-icing on a Svalbard reindeer population: Results of a simple snowpack model. *Arctic Antarctic and Alpine Research* **36:** 333-341.

Kojola, I., Helle, T., Huhta, E., & Niva, A. (1998). Foraging conditions, tooth wear and herbivore body reserves: a study of female reindeer. *Oecologia* **117:** 26-30.

Koubek, P. & Zima, J. (1999). *Cervus elaphus*. In *The Atlas of European Mammals* : 388-389. Mitchell-Jones, A. J., Amori, G., Bogdanovics, W., Krysstufek, B., Reijnders, P. J. H., Spitzenberger, F., Stubbe, M., Thissen, J. B. M., Vohralik, V. & Zima, J. (Ed.). London, UK: Academic Press.

Kruuk, L. E. B., Slate, J., Pemberton, J. M., Brotherstone, S., Guinness, F., & Clutton-Brock, T. (2002). Antler size in red deer: Heritability and selection but no evolution. *Evolution* **56:** 1683-1695.

Langer, P. (1988). *The mammalian herbivore stomach: comparative anatomy, function and evolution*. Stuttgart; New York: Gustav Fischer Verlag.

Langvatn, R. (1999). Hjortens erobring av Norge. In *Brennpunkt Natur 98/99*: 49-71. Brox, K. H. (Ed.). Trondheim, Norway: Tapir forlag.

Langvatn, R., Mysterud, A., Stenseth, N. C., & Yoccoz, N. G. (2004). Timing and synchrony of ovulation in red deer constrained by short northern summers. *American Naturalist* **163:** 763-772.

Lechner-Doll, M., Kaske, M., & Engelhardt, W. V. (1991). Factors affecting the mean retention time of particles in the forestomach of ruminants and camelids. In *Physiological aspects of digestion and metabolism in ruminants.*: 455-482. Tsuda, T., Sasaki, Y. & Kawashima, R. (Ed.). San Diego, CA: Harcourt Brace Jovanovich.

Loe, L. E., Mysterud, A., Langvatn, R., & Stenseth, N. C. (2003). Decelerating and sex-dependent tooth wear in Norwegian red deer. *Oecologia* **135:** 346-353.

Logan, M. & Sanson, G. D. (2002). The effect of tooth wear on the feeding

behaviour of free-ranging koalas (*Phascolarctos cinereus*, Goldfuss). *Journal of Zoology* **256:** 63-69.

Loison, A., Cuyler, L. C., Linnell, J. D. C., & Landa, A. (2001). Sex, age, condition and tooth wear of harvested caribou *Rangifer tarandus groenlandicus* in west Greenland, 1995-1998. *Wildlife Biology* **7:** 263-273.

Loison, A., Langvatn, R., & Solberg, E. J. (1999). Body mass and winter mortality in red deer calves: disentangling sex and climate effects. *Ecography* **22:** 20-30.

Lucas, P. W. (2004). *Dental functional morphology*. Cambridge, UK: Cambridge University Press.

Luke, D. A. & Lucas, P. W. (1983). The significance of cusps. *Journal of Oral Rehabilitation* **10:** 197-206.

Masoro, E. J. (2000). Caloric restriction and aging: an update. *Experimental Gerontology* **35:** 299-305.

Mathiesen, S. D. (1999). *Comparative aspects of digestion in reindeer: digestive adaptations in reindeer on South Georgia and in Northern Norway (Rangifer tarandus tarandus) and in Svalbard reindeer (Rangifer tarandus platyrhynchus)*. Thesis: Department of Arctic Biology and Institute of Medical Biology, University of Tromsø; Department of Arctic Veterinary Medicine, Norwegian School of Veterinary Science, Tromsø.

Merceron, G., Viriot, L., & Blondel, C. (2004). Tooth microwear pattern in roe deer (*Capreolus capreolus* L.) from Chize (Western France) and relation to food composition. *Small Ruminant Research* **53:** 125-132.

Mysterud, A., Langvatn, R., Yoccoz, N. G., & Stenseth, N. C. (2001a). Plant phenology, migration and geographical variation in body weight of a large herbivore: the effect of a variable topography. *Journal of Animal Ecology* **70:** 915-923.

Mysterud, A., Yoccoz, N. G., Stenseth, N. C., & Langvatn, R. (2001b). Effects of age, sex and density on body weight of Norwegian red deer: evidence of density-dependent senescence. *Proceedings of the Royal Society of London Series B-Biological Sciences* **268:** 911-919.

Nussey, D. H., Metherell, B., Moyes, K., Donald, A., Guinness, F. E., & Clutton-Brock, T. H. (2007). The relationship between tooth wear, habitat quality and late-life reproduction in a wild red deer population. *Journal of Animal Ecology* **76:** 402-412.

Perez-Barberia, F. J., Elston, D. A., Gordon, I. J., & Illius, A. W. (2004). The evolution of phylogenetic differences in the efficiency of digestion in ruminants. *Proceedings of the Royal Society of London Series B-*

Biological Sciences **271:** 1081-1090.

Perez-Barberia, F. J. & Gordon, I. J. (1998a). Factors affecting food comminution during chewing in ruminants: a review. *Biological Journal of the Linnean Society* **63:** 233-256.

Perez-Barberia, F. J. & Gordon, I. J. (1998b). The influence of molar occlusal surface area on the voluntary intake, digestion, chewing behaviour and diet selection of red deer (*Cervus elaphus*). *Journal of Zoology* **245:** 307-316.

Perez-Barberia, F. J. & Gordon, I. J. (1999). The functional relationship between feeding type and jaw and cranial morphology in ungulates. *Oecologia* **118:** 157-165.

Pettorelli, N., Gaillard, J. M., Mysterud, A., Duncan, P., Stenseth, N. C., Delorme, D., Van Laere, G., Toigo, C., & Klein, F. (2006). Using a proxy of plant productivity (NDVI) to find key periods for animal performance: the case of roe deer. *Oikos* **112:** 565-572.

Pettorelli, N., Mysterud, A., Yoccoz, N. G., Langvatn, R., & Stenseth, N. C. (2005). Importance of climatological downscaling and plant phenology for red deer in heterogeneous landscapes. *Proceedings of the Royal Society of London Series B-Biological Sciences* **272:** 2357-2364.

Reimers, E. & Ringberg, T. (1983). Seasonal changes in body weights of Svalbard reindeer from birth to maturity. *Acta Zoologica Fennica* **175:** 69-72.

Rensberger, J. M. (1973). Occlusion model for mastication and dental wear in herbivorous mammals. *Journal of Paleontology* **47:** 515-528.

Rensberger, J. M. (1988). The transition from insectivory to herbivory in mammalian teeth. In *Teeth revisited: Proceedings of the 7th International Symposium on Dental Morphology, Paris*: 351-365. Russell, D. E., Santoro, J. P. & Sigogneau-Russell, D. (Ed.).

Røed, K. H., Staaland, H., Broughton, E., & Thomas, D. C. (1986). Transferrin variation in caribou *Rangifer-tarandus* on the Canadian Arctic Islands. *Canadian Journal of Zoology* **64:** 94-98.

Sansoni, G., Carocci, M., & Rodella, R. (1999). Three-dimesional vision based on a combination of gray-code and phase-shift light projection: analysis and compensation of the systematic errors. *Applied Optics* **38:** 6565-6573.

Schmölcke, U. & Zachos, F. E. (2005). Holocene distribution and extinction of the moose (*Alces alces, Cervidae*) in Central Europe. *Mammalian Biology* **70:** 329-344.

Scott, R. S., Ungar, P. S., Bergstrom, T.

S., Brown, C. A., Grine, F. E., Teaford, M. F., & Walker, A. (2005). Dental microwear texture analysis shows within-species diet variability in fossil hominins. *Nature* **436:** 693-695.

Short, R. V. & Hay, M. F. (1966). Delayed implantation in the roe deer (*Capreolus capreolus*). *Symposium of the Zoological Society of London* **15:** 173-194.

Sinclair, D. A. (2005). Toward a unified theory of caloric restriction and longevity regulation. *Mechanisms of Ageing and Development* **126:** 987-1002.

Skogland, T. (1988). Tooth wear by food limitation and its life-history consequences in wild reindeer. *Oikos* **51:** 238-242.

Solberg, E. J., Jordhøy, P., Strand, O., Aanes, R., Loison, A., Sæther, B.-E., & Linnell, J. D. C. (2001). Effects of density-dependence and climate on the dynamics of a Svalbard reindeer population. *Ecography* **24:** 441-451.

Solberg, E. J., Rolandsen, C. M., Heim, M., Grøtan, V., Garel, M., Sæther, B.-E., Nilsen, E. B., Austrheim, G., & Herfindal, I. (2006). *Elgen i Norge sett med jegerøyne - En analyse av jaktmaterialet fra overvåkingsprogrammet for elg og det samlede sett elg-materialet for perioden 1966-2004*. Trondheim: Norwegian Institute for Nature Research.

Solberg, E. J., Sæther, B.-E., Strand, O., & Loison, A. (1999). Dynamics of a harvested moose population in a variable environment. *Journal of Animal Ecology* **68:** 186-204.

Solounias, N., Fortelius, M., & Freeman, P. (1994). Molar wear rates in ruminants - a new approach. *Annales Zoologici Fennici* **31:** 219-227.

Sørmo, W., Haga, O. E., Gaare, E., Langvatn, R., & Mathiesen, S. D. (1999). Forage chemistry and fermentation chambers in Svalbard reindeer (*Rangifer tarandus platyrhynchus*). *Journal of Zoology* **247:** 247-256.

Spalinger, D. E. & Robbins, C. T. (1992). The dynamics of particle flow in the rumen of mule deer (*Odocoileus hemionus hemionus*) and elk (*Cervus elaphus nelsoni*). *Physiological Zoology* **65:** 379-402.

Stearns, S. C. (1992). *The Evolution of Life Histories*. New York: Oxford University Press Inc.

Teaford, M. F. (1988). A review of dental microwear and diet in modern mammals. *Scanning Microscopy* **2:** 1149-1166.

Teaford, M. F., Smith, M. M., & Ferguson, M. W. J. (2000). *Development, function, and evolution of teeth*. New York: Cambridge University Press.

Tyler, N. J. C. (1987). *Natural limitation*

of the abundance of the High Arctic Svalbard reindeer. PhD Thesis. Cambridge University.

Van der Knaap, W. O. (1986). On the presence of reindeer (*Rangifer tarandus* L.) on Edgeoya, Spitsbergen, in the period 3800-5000 BP. *Circumpolar Journal* **1:** 3-9.

Van der Wal, R., Madan, N., Van Lieshout, S., Dormann, C., Langvatn, R., & Albon, S. D. (2000). Trading forage quality for quantity? Plant phenology and patch choice by Svalbard reindeer. *Oecologia* **123:** 108-115.

Van Soest, P. J. (1994). *Nutritional ecology of the ruminant.* Cornell University Press.

Walker, A., Hoeck, H. N., & Perez, L. (1978). Microwear of mammalian teeth as an indicator of diet. *Science* **201:** 908-910.